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Variability and Significance of Parietal and Ventral Scales in the Marine Snakes of the Genus *Lapemis* (Serpentes: Hydrophiidae), with Comments on the Occurrence of Spiny Scales in the Genus

Paul Gritis

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Variability and Significance of Parietal and Ventral Scales in the Marine Snakes of the Genus *Lapemis* (Serpentes: Hydrophiidae), with Comments on the Occurrence of Spiny Scales in the Genus

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Accepted December 1, 1988

Published June 29, 1990

Publication 1411

PUBLISHED BY FIELD MUSEUM OF NATURAL HISTORY

© 1990 Field Museum of Natural History
ISSN 0015-0754
PRINTED IN THE UNITED STATES OF AMERICA

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Variability and Significance of Parietal and Ventral Scales in Marine Snakes of the Genus *Lapemis* (Serpentes: Hydrophiidae), with Comments on the Occurrence of Spiny Scales in the Genus

Abstract

Over 1,400 specimens referred to the two nominate forms of *Lapemis*, from throughout the range, were examined for condition of the parietal and ventral scales. The state of these scales has been considered a diagnostic character separating the two species. Observed frequencies of the character states demonstrate a continuum of variation through much of the geographic range. We conclude that all *Lapemis* belong to a single species, *L. curtus*. Possible adaptive values for the scale characters are discussed.

Introduction

Marine snakes of the genus *Lapemis* are widely distributed (fig. 1) and are very often a dominant component of the hydrophiid fauna of a region (Tu, 1974; Redfield et al., 1978; Voris & Voris, 1983). Typically two species are recognized (Smith, 1926; Minton, 1975; Voris, 1977). McDowell (1972) expanded the genus to include *Kolpophis annandalei* and *Thalassophina viperina*. However, *Kolpophis* differs from *Lapemis* in numbers of dorsal scale rows and ventrals (Burger & Natsuno, 1974). Further, since McDowell (1972) did not list the specimens he examined and did not provide data on localities sampled, or furnish the number of *Lapemis* examined, we feel that his data, as published, are inadequate for taxonomic conclusions.

Smith (1926) distinguishes the two species on the basis of the condition (fragmented or entire) of the parietal and ventral scales and places them allopatrically with *L. curtus* in the Indian Ocean

and *L. hardwickii* in southeast Asian and Australian waters. Aspects of the parietal and ventral scales are the only characters that have consistently been used to distinguish the two species (e.g., Smith, 1926).

Previous investigators have noted the occurrence of anomalous parietal and ventral scales in specimens of *Lapemis*, resulting in *curtus*-like forms being reported from the *hardwickii* portion of the range and vice-versa (Laidlaw, 1901, p. 580; Wall, 1906, p. 295, 1909, p. 246, 1921, pp. 415, 419; Boulenger, 1912, p. 192; Smith, 1926, pp. 110, 113; Bourret, 1935, p. 54). Smith (1926, p. 110) regarded some of these specimens as "aberrant individuals"; however, we hypothesized that these reports suggested the existence of unassessed variability in these taxonomically important characters.

The purpose of this paper is to evaluate variability in the parietal and ventral scales in snakes of the genus *Lapemis*. Because other scale characters have not been found to be useful in distinguishing the two species, they will not be considered in this paper.

Materials and Methods

Over 1,400 museum specimens (see Appendix) of *Lapemis* were scored for the following data: snout-vent length (svl) and tail length, each to the nearest .5 cm; sex; and condition of the parietal and ventral scales.

The parietal condition for each snake was scored as a single character state. A total of 22 states was found; for ease of manipulation, phenetically similar states were grouped together, yielding a work-

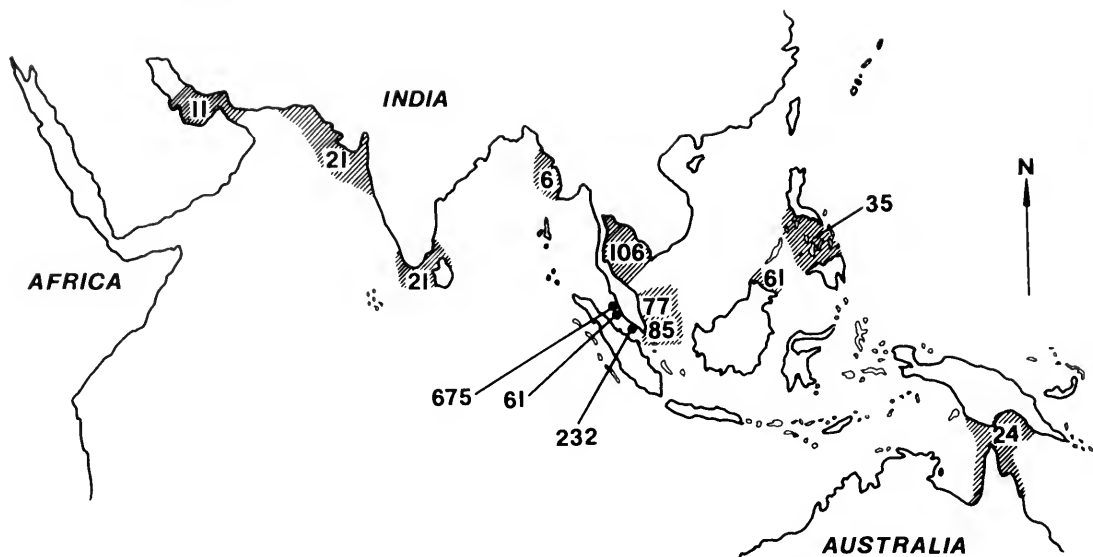


FIG. 1. Localities and sample sizes for *Lapemis* examined. Shading indicates extent of collection area. Malaysian localities are: Sungei Buloh (675), Sekinchang (61), Parit Botak (232), Mersing (77), Singapore (85).

ing set of seven classes (fig. 2). Snakes with damaged parietals were not included.

Each snake was scored for ventral scale condition at each of three body regions: anterior third of svl; midbody third of svl; and posterior third of svl. The predominant condition of the ventrals at each of these three body regions was recorded (a body region may have two or more states present). To facilitate analysis the 10 observed ventral

states were grouped into 5 classes, each consisting of phenetically similar states (fig. 3). Snakes with midventral incisions that obliterated the ventral scales were not scored.

The data were organized by locality (table 1). For each of five of the largest samples the data were also sorted by sex and by size. Two size classes were used: 49.5 cm svl and below, and 50.0 cm svl and above. *Lapemis* neonates are relatively

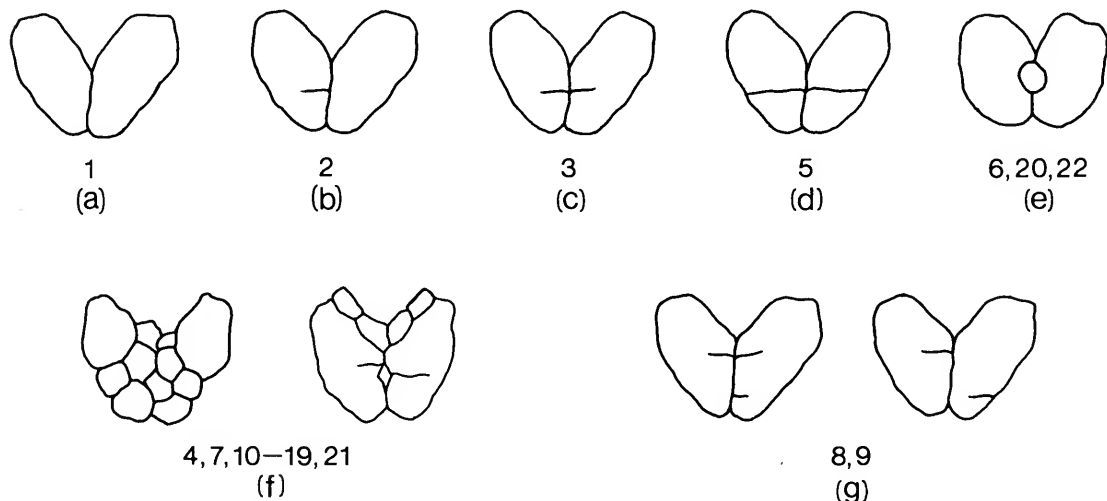


FIG. 2. Parietal scale character states in *Lapemis*. The observed states (1–22) are grouped into seven phenotypically similar classes (a–g). a, parietals unbroken; b, one parietal fractured; c, both parietals fractured for half or less of their width; d, both parietals fractured for more than half their width; e, formation of median scales; f, extensive fracturing; g, > 1 fracture per scale, or asymmetric fracturing. Not drawn to scale.

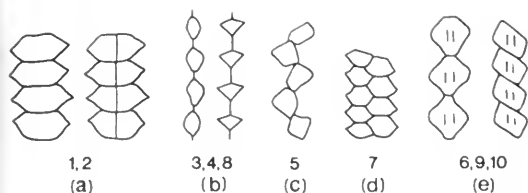


FIG. 3. Ventral scale states in *Lapemis*. The observed states (1–10) are grouped into five phenotypically similar classes (a–e). Median suture shown in state 2. Paired spines are shown on scales in class e (see text). Not drawn to scale.

large. They have been recorded as ranging from 330 to 355 mm (Wall, 1921; whether svl or total length not given); 25 to 30 cm (Halstead et al., 1978; svl or total length not given); and about 25.0 cm svl (Voris, unpubl. data) and about 23.5 g mean weight (Lemen & Voris, 1981). Females may be sexually mature at 44.9 cm (Bergman, 1949, p. 885), although recent work (Voris, unpubl. data) suggests that a figure of 50.0 cm svl may be more typical.

Frequency distributions of parietal and ventral scale states at the 13 localities were compared using the chi-square test. The level of significance considered meaningful was $P < .01$ or less, owing to the fact that multiple (69) nonindependent tests were run when comparing the populations at the various localities.

Results

Sexual Dimorphism

Sexual dimorphism in each character was examined at five localities represented by large samples. For the parietal scales, significant between-sex differences were found at three localities (Singapore, $P < .02$; Sungei Buloh, $P < .005$; Parit Botak, $P < .005$). At these three localities, the following trends occur. Intact parietals (fig. 2a) are about twice as common among males as females. The females exhibit the fractured parietal condition (figs. 2e,f, 4) more frequently than do the males, with ratios ranging from 2:1 to 5:1. No significant differences were found at Borneo or Thailand, although the above trends seem to hold.

The anterior ventral scales were significantly different at four localities (Singapore, $P < .01$; Thailand, $P < .005$; Sungei Buloh, $P < .001$; Parit Botak, $P < .001$). The males exhibited a higher



FIG. 4. Dorsum of head of Australian *Lapemis* (AMNH 87679) showing fragmented parietal scales here considered class "f" (see text and fig. 2).

proportion of fragmented, shifted ventrals (fig. 3c) than females, with ratios ranging from about 1.5:1 to 7:1. The females had intact ventral scales (fig. 3a) more often than did males, with ratios ranging from 1:1 to 11:1, although at any given locality only 22% or less of the females exhibited that state.

Populations from all five localities showed highly significant between-sex differences in ventral scale characters at the midbody region ($P < .005$ –.001). As with the anterior body region, ventral scales that retained the typical ventral scale shape, although reduced in size (figs. 3a,e), were more common among females than males, with ratios ranging from 2:1 to 20:1. This is true despite the fact that many (5–46%) of the females at any locality have ventral scales indistinguishable from the body scales (fig. 3d). Males showed a high frequency (57–76%) of fractured ventrals much smaller than the adjacent body scales (fig. 3b), with ratios ranging from 3:1 to 36:1.

None of the five localities showed significant

TABLE 1. Observed distribution of parietal and ventral scale character state classes in the *Lapemis* examined. The localities are plotted and the sample sizes are given in Figure 1.

Char- acter states	Persian Gulf	Arabian Sea	S. India-Ceylon	Burma	Thailand	Philippines	North Borneo	Singapore	Mersing	Sekinchang	Sungei Buloh	Parit Botak	Australia
Parietals													
a	—	—	—	1	56	7	11	27	26	16	121	83	3
b	—	—	—	1	8	3	8	10	3	4	66	23	—
c	—	—	—	—	21	18	26	19	27	29	329	75	4
d	1	3	3	1	—	—	—	—	—	—	13	—	—
e	—	—	—	—	12	2	2	19	7	4	47	22	6
f	9	18	18	3	8	4	6	3	12	8	66	17	9
g	1	—	—	—	1	—	5	—	2	—	8	1	1
Total	11	21	21	6	106	34	58	78	77	61	650	221	23
Anterior ventrals													
a	10	21	21	3	10	14	15	7	13	7	55	34	2
b	—	—	—	1	22	3	16	12	19	7	133	48	2
c	—	—	—	1	22	2	7	23	15	11	196	42	5
d	—	—	—	—	32	11	8	19	7	10	130	42	3
e	—	—	—	1	18	5	15	24	23	26	158	61	12
Total	10	21	21	6	104	35	61	85	77	61	675	227	24
Midbody ventrals													
a	9	17	13	2	4	4	6	3	—	3	32	10	1
b	—	—	—	3	50	15	23	23	33	23	297	97	12
c	—	—	—	—	8	3	5	13	21	8	103	37	2
d	—	—	5	—	31	7	6	13	8	3	89	36	4
e	1	4	3	1	11	6	21	33	15	24	148	52	5
Total	10	21	21	6	104	35	61	85	77	61	670	232	24
Posterior ventrals													
a	7	6	7	2	20	14	25	21	23	16	281	89	8
b	—	—	—	—	78	—	—	—	—	—	—	—	—
c	—	—	—	—	—	—	1	—	—	—	1	1	—
d	2	12	9	3	—	20	34	54	51	31	362	137	16
e	1	3	4	1	4	—	1	7	3	13	28	4	—
Total	10	21	20	6	102	34	61	82	77	60	671	231	24

sexual differences in the ventral scales from the posterior third of the svl.

Ontogenetic Variation

The distribution of parietal and ventral states was examined for two size classes, juvenile and adult, in the same five large samples studied for sexual dimorphism (see previous section). No significant differences in parietal state distribution between juveniles and adults were found at these localities.

Many significant differences were found for ventral state distributions. At the anterior svl region, three localities showed significant age-specific dif-

ferences in ventral state characters (Singapore, $P < .005$; Sungei Buloh, $P < .001$; Parit Botak, $P < .001$). Fractured ventrals (fig. 3b) are about twice as common among the young as among the adults, while the adults often (37–47%) showed ventrals reduced in size but unchanged in shape (fig. 3e).

At the midbody region, only Sungei Buloh and Parit Botak showed significant ($P < .001$) age-specific differences. The juveniles usually (46–53%) had more fragmented ventrals (fig. 3b) than did the adults (1.2:1–1.7:1). About twice as many adults as juveniles showed ventrals reduced in size (fig. 3e).

At the posterior body region we found significant differences ($P < .005$) in ventral scale frequencies in the samples from Sungei Buloh and

Borneo. Juveniles had higher numbers of ventrals indistinct from body scales (fig. 3d) than did the adults (1.2:1–2.3:1). Adults from Borneo showed over four times as many large intact ventrals as did the Bornean juveniles; at Sungei Buloh the observed ratio was very near 1:1.

Geographic Variation

PARIETALS—The number of snakes with each of the parietal scale states is given in Table 1, and frequency distributions within each locality are presented in Figure 5.

The frequency distributions of parietals of those *Lapemis* from the westernmost localities (Persian Gulf, Arabian Sea, India) are all similar to each other and are significantly ($P < .001$) different from all other localities except for Burma and Australia (fig. 7). The Burmese sample was not significantly different from the Persian Gulf sample, and differed from both the Arabian Sea and the Indian material at the .05 level. Samples from Australia and the Persian Gulf were significantly different at the .05 level. The Burmese and Australian samples were not statistically different.

The samples from Thailand, peninsular Malaysia, Borneo, and the Philippines were often significantly different ($P < .005$) from each other. Highly fragmented parietals (figs. 2d,f,g, 4) are very common (68–100%) in the four westernmost samples (including Burma). From the Straits of Malacca eastward, two parietal states are common (13–53%): intact parietals (fig. 2a) and parietals with a transverse suture (fig. 2c).

ANTERIOR VENTRALS—The specimens from the Persian Gulf, Arabian Sea, and Indian localities show large intact ventrals (fig. 3a) only. Half of the Burmese specimens show intact ventrals, the remainder various degrees of fragmentation or reduction. Most of the remaining samples are not significantly different from each other, but do differ ($P < .001$) from the above mentioned localities with large intact ventrals. The sample from the Philippines, with its high frequency of intact ventrals, differs from all the Malaysian and southeast Asian localities ($P < .05$ –.001) and is not distinct from the Burmese sample.

MIDBODY VENTRALS—The samples from the Persian Gulf, the Arabian Sea, and India are different from the Burmese sample ($P < .05$) and also from all the other samples ($P < .001$). The sample from Thailand is distinct ($P < .001$) from all of the Malaysian samples because of its higher fre-

quency of ventrals indistinguishable from the body scales (fig. 3d) and lower frequency of ventrals that are not fragmented but are reduced in size (fig. 3e).

POSTERIOR VENTRALS—Many of the samples that were statistically different at the anterior and mid-body regions were not different at the posterior svl region. Fewer character states were observed in this body region. Most localities lacked individuals showing fragmented ventrals (figs. 3b,c). In the Thai sample, however, 77% of the *Lapemis* showed class b ventrals; of the ca. 1,300 individuals in the other 12 localities, none exhibited class b ventrals and only 3 were grouped into class c. The Thai sample was thus highly ($P < .001$) distinct from all other samples for the posterior ventrals.

Discussion

Taxonomy

We conclude that our data for the parietal and ventral scales do not support a species distinction between *L. curtus* and *L. hardwickii*.

According to the generally accepted dichotomy (e.g., Smith, 1926) the parietal scales should occur in two states, correlated with geography as follows: parietals fragmented in specimens from the Persian Gulf eastwards to the western Malaysian peninsula (*L. curtus*), and parietals usually entire in specimens ranging from the Straits of Malacca to Australia (*L. hardwickii*). We did not observe such a clear-cut distribution of parietal states.

The samples from the Persian Gulf, the Arabian Sea, and India fit the pattern for *L. curtus*, with the observed values for fragmented parietals (figs. 2d,f) ranging from 91 to 100% (table 1). The Burmese material was significantly different ($P < .05$) from the Arabian Sea and Indian material. Comparisons between these four localities and the remaining localities were, with one exception, significantly different ($P < .05$ –.005). That exception was the comparison between the Persian Gulf and Australia, which, although significant at the .05 level, nevertheless was less different than might have been expected for the two endpoints of a wide geographic distribution (fig. 1). The Australian sample was most similar to the Burmese sample, and with the exception of Mersing ($P < .01$) was highly significantly different ($P < .005$) from all other east Asian (i.e., *L. hardwickii*) localities with which it would be expected to show the greatest

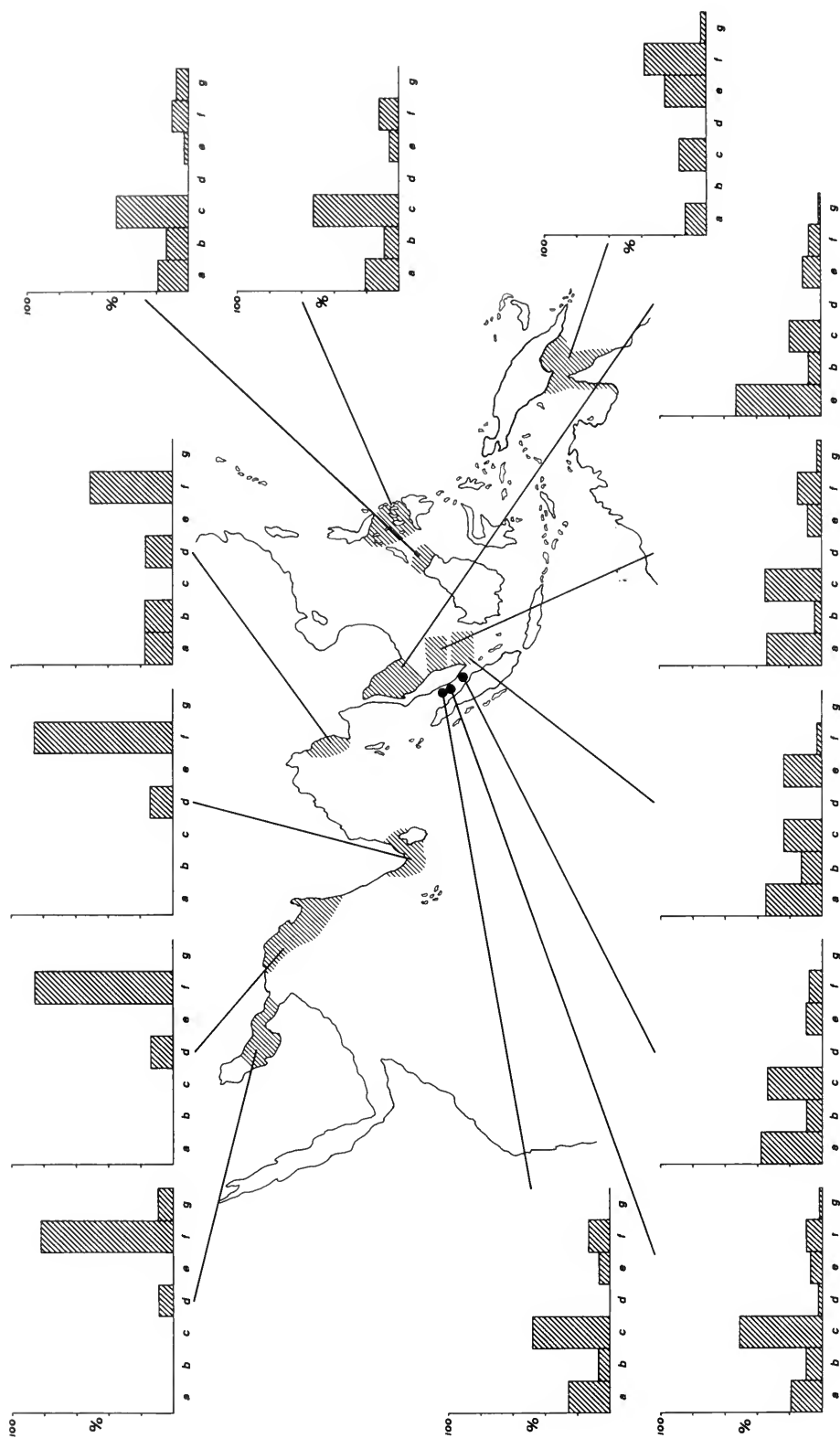


FIG. 5. Frequency distributions of parietal scale character state classes in *Lapemis*. Scale states are illustrated in Figure 2. Actual values are given in Table 1.

similarity. This tendency of Australian *Lapemis* to exhibit fractured parietals has been noted (Worrell, 1963) and fractured parietals have also been figured (Cogger, 1979, photo 784; Storr et al., 1986, p. 169).

The Australian sample, therefore, approaches *L. curtus* in parietal scale morphology more closely than it does *L. hardwickii*. The non-Australian, east Asian samples are very different from those samples that do approach the *L. curtus* condition (fig. 5), yet they are also very different from the predicted values for typical *L. hardwickii*. Typical *L. hardwickii* by definition show "undissected" or "entire" parietals only—i.e., a frequency of 100% for this class (fig. 2a). The Thai sample shows a frequency of only 53% for entire parietals, and all of the other samples from localities within the range of *L. hardwickii* show frequencies of only 13–38%. Thus, between 47% and 87% of all the *Lapemis* at any of these localities do not show the expected parietal state condition. The majority of the observed fragmentation is partial transverse dissection of the parietals (fig. 2c), which in appearance is intermediate between intact parietals and completely dissected parietals.

The differences between southeast Asian (i.e., *L. hardwickii*) localities are often highly significant. For example, comparisons of Thailand with Borneo, Singapore with Sungei Buloh, and Parit Botak with Australia are all highly significant ($P < .001$). These large differences between, in some cases, adjacent localities suggest that the condition of the parietals is limited in its usefulness as a taxonomic character.

The ventral scales are not as easily studied as are the parietals because there are many ventrals in each body region of each snake, and usually there is more than one ventral state present. The expected condition of ventrals, according to Smith (1926) would be: ventrals intact throughout in specimens from the Persian Gulf, Arabian Sea, India, and Burma (*L. curtus*); and ventrals very small or absent posteriorly in east Asian specimens (*L. hardwickii*).

Our observations on the ventrals of the anterior body region uphold this prediction. Those specimens from the westernmost localities show predominantly entire ventrals, those from the other localities chiefly fragmented ventrals (table 1; fig. 6).

Fragmented ventrals occur more frequently in the midbody region than in the anterior body region at all localities examined (table 1). This also agrees with Smith's (1926) description. The Thai

sample differs significantly ($P < .005$) from most of the other southeast Asian localities because of the low frequency of ventrals reduced in size but unchanged in shape (fig. 3c). Most of the other east Asian samples were not significantly different from each other (fig. 7).

The posterior third of the svl is reported to typically show ventral scale fragmentation in both *L. curtus* and *L. hardwickii*, and especially in the latter (Smith, 1926). Our data from the westernmost localities fit this prediction, with 30–71% of the snakes from the Persian Gulf, Arabian Sea, India, and Burma having fragmented ventrals.

The snakes from the east Asian localities are surprising in that they approach the standard *L. curtus* ventral condition, i.e., large, entire ventrals occur frequently in Borneo (41%), the Philippines (41%), Sungei Buloh (42%), and Thailand (20%). Indeed, large ventrals occur at these localities often enough so that many comparisons between *L. curtus* localities and *L. hardwickii* localities are not significantly different (fig. 8).

It may be noted that sample sizes from the western part of the range were smaller than most other samples. Collections have rarely been made in these areas (e.g., Persian Gulf, Burma) and collection in the near future is unlikely.

We conclude that the observed variability of the parietal and ventral scales suggests that the snakes of the genus *Lapemis* belong to a single polymorphic species rather than to two sibling species. We do not recognize subspecies and assign all specimens to *L. curtus* (Shaw).

Comments on Scalation and Spines in *Lapemis*

Much variation exists in the scale characters that we examined in *Lapemis*. We will comment here on the extent and source of this variability, its possible adaptive value, and also discuss briefly the epidermal spines associated with the scales of *Lapemis*.

Fragmentation of parietal scales, widespread in *Lapemis*, occurs in varying degrees in other hydrophiids, e.g., *Emydocephalus ijimae*, *Thalosophis* (= *Kolpophis*) *annandalei*, *T. anomalus*, *Hydrophis caeruleus*, and *Astrotia stokesi* with highly fragmented parietals in *Acalyptus* (= *Acalyptophis*) (Wall, 1909; Cogger, 1975). *Pelamispaturus* may also exhibit fragmented parietals (Friederich, 1978, fig. 49; Mao & Chen, 1980, fig.

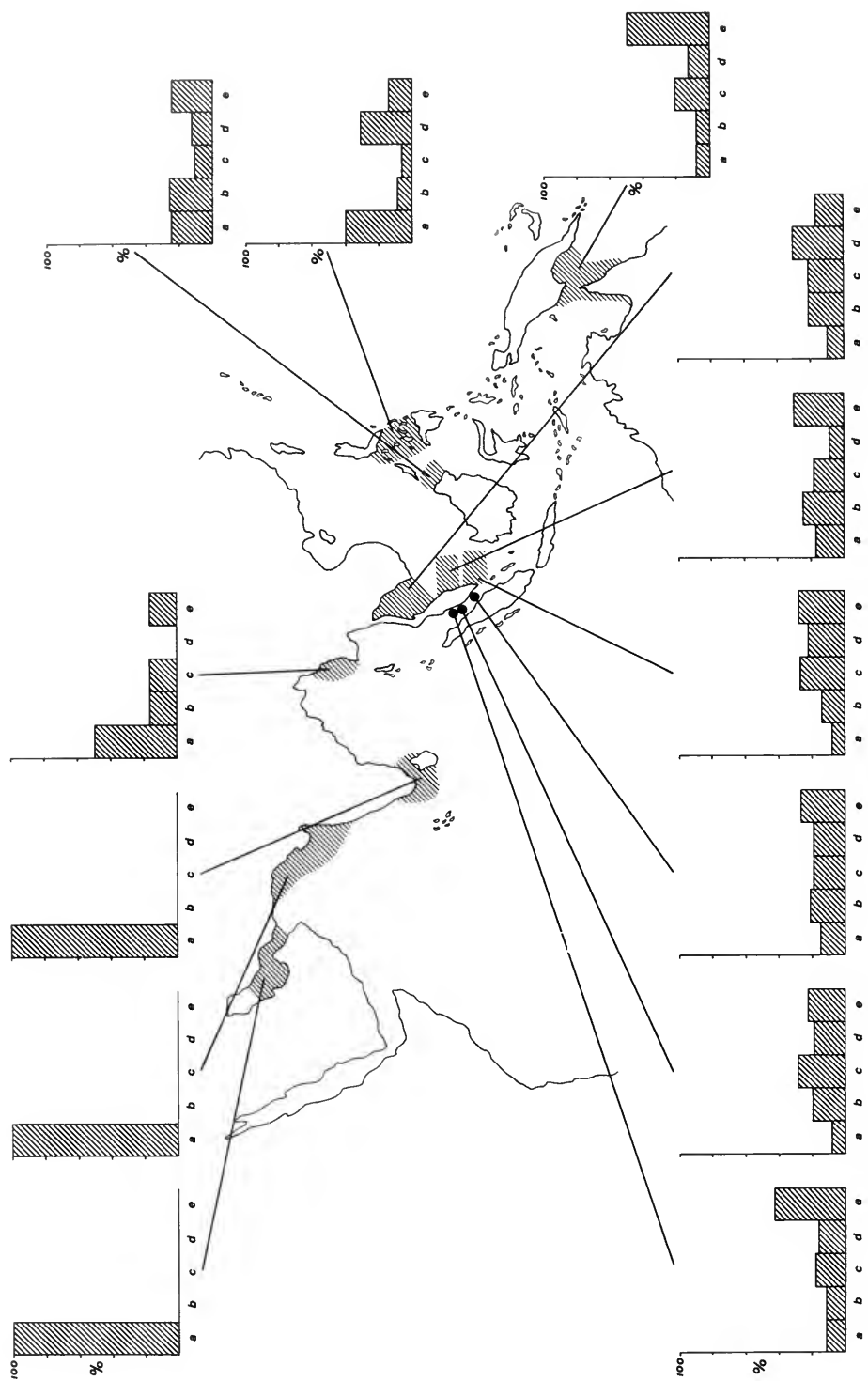


FIG. 6. Frequency distributions of anterior ventral scale character state classes in *Lapetus*. Scale states are illustrated in Figure 3. Actual values are given in Table 1.

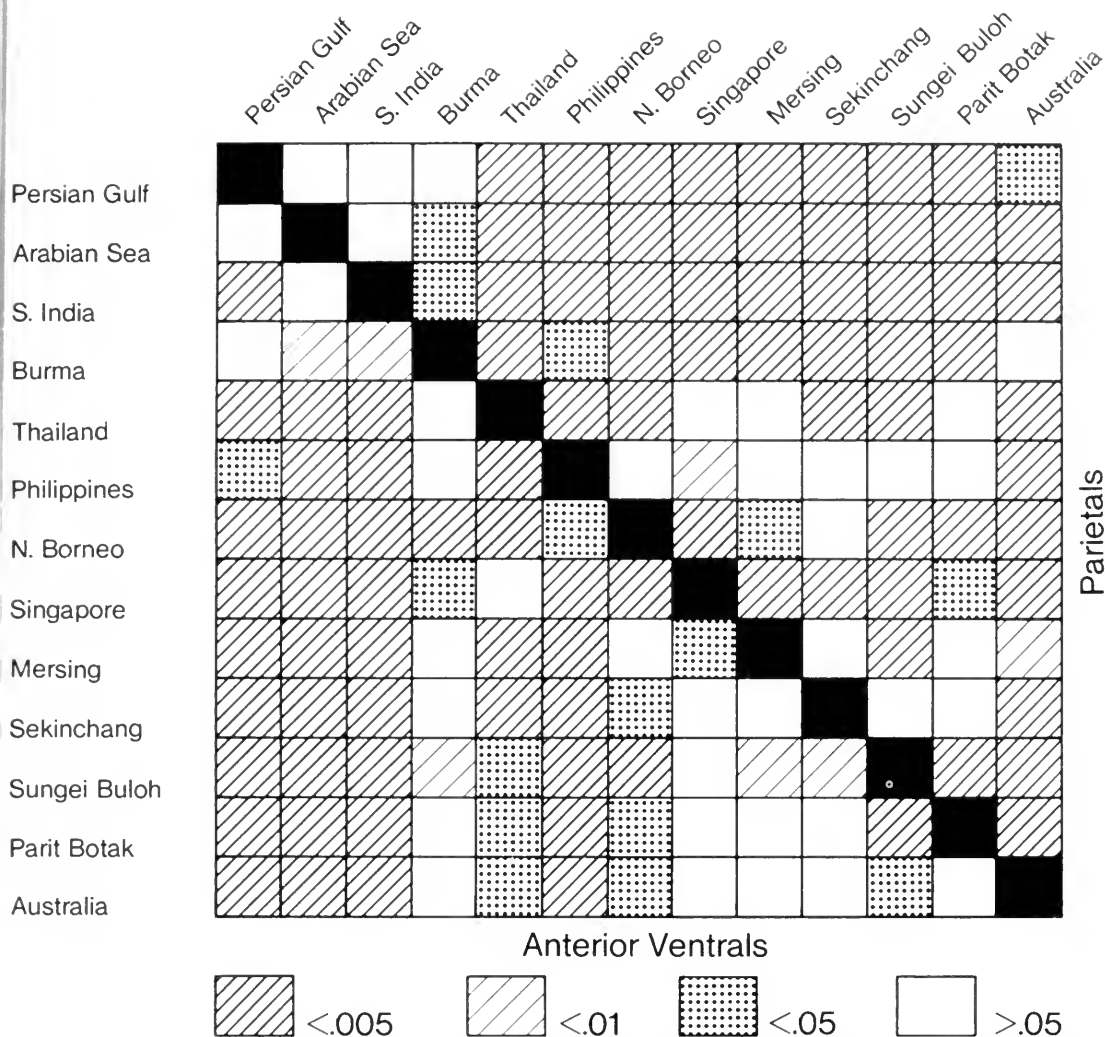


FIG. 7. Results of chi-square tests for comparisons between geographic localities of the frequency distributions of parietal and anterior ventral scale character states presented in Table 1. Numerical values are significance levels ($P <$).

33) as may some species of *Aipysurus* (Cogger, 1975; Friederich, 1978). Parietal fragmentation is less frequent in colubrids, occurring in *Dityophis vivax* (Gunther, 1881), *Pythonodipsas carinata*, and *Spalerosophis diadema* (Marx et al., 1982). Fragmentation of the parietals (and other head plates) is common among the Boidae, Viperidae, and Crotalidae (Marx & Rabb, 1972).

Head plate fragmentation may occur as a congenital condition (Reichenbach-Klinke & Elkan, 1965, fig. 394; Secoy, 1970). It has usually been asserted to be adaptive for the increased kinesis required to increase gape or for fang erection (e.g., Viperidae) (Marx & Rabb, 1972; Friederich, 1978;

Marx et al., 1982; Pough & Groves, 1983). Although *Lapemis* has fixed fangs, it is a generalist feeder (Voris & Voris, 1983) and so may benefit from any increase in gape permitted by increased flexibility of cranial skin. In the present study, we did not observe any significant differences in parietal scale state distribution between young and adults, suggesting that there may not be strong ontogenetic selection for fragmented parietals.

Fragmentation of ventral scales also occurs in many other sea snakes (see Smith, 1926, plate 1). It has been noted as an aberrant condition or developmental anomaly in colubrids (Underwood, 1948; King, 1959; Clark & Callison, 1967; Fritts,

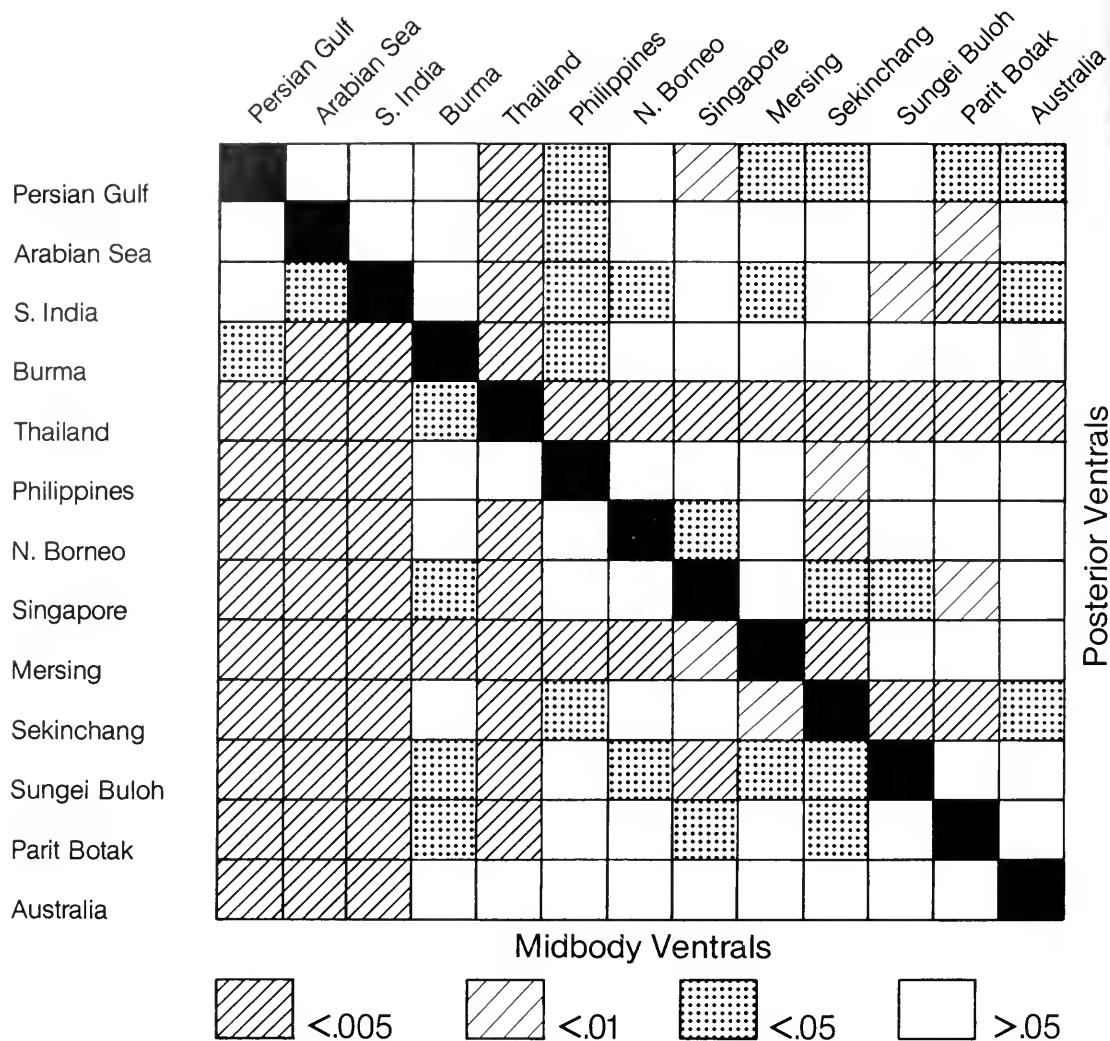


FIG. 8. Results of chi-square tests for comparisons between geographic localities of the frequency distributions of midbody and posterior ventral scale character states presented in Table 1. Numerical values are significance levels ($P <$).

1968; Plummer, 1980) and in boids (Frye, 1981, p. 315), and as such it has not been used by these authors as a taxonomic character. Widespread ventral fragmentation within the Dipsadinae has been noted by Peters (1960, pp. 10–12).

There is generally a 1:1 correspondence between ventral scale number and vertebral number in Colubroids with some exceptions, including *Lapemis* (Voris, 1975). These exceptions are due to an increase in the number of ventral scales. Loss of functional correspondence in muscle-scale relationships may lead to increased variability (Voris & Jayne, 1976) while the number of vertebrae tends to remain stable (Voris, 1975).

Voris (1975) has suggested that the reduction in size and increase in number of ventral scales may be adaptive for the following reasons: (1) allowing the deepening of the body presumed advantageous for aquatic lateral undulation; (2) increased expandability (hence capacity) of the gut region; and (3) increased expandability of the body during gestation. This last reason is supported by the observation that females have higher ventral counts and more dorsal scale rows than do males (Smith, 1926; Voris, 1975).

The cause of the variability in the parietal and ventral scales is unknown. Experimental studies have shown that the temperature during embry-

onic development can affect meristic characters (Fox, 1949; Vinegar, 1974; Osgood, 1978). A correlation of low temperature with low number of body annuli (= number of vertebrae) has been presented for amphisbaenids (Vanzolini, 1968) although small, regular increments in temperature do not appear to be correlated with small, regular increments in numbers of scales (Gans, 1977). Because fragmented parietals and ventrals are found throughout the range of *Lapemis* and in collections made at different times, it is unlikely that these all represent environmentally induced developmental anomalies. The extensive variation observed suggests the lack of strong selection for a narrow range of parietal and ventral conditions.

The spiny scales of *Lapemis* have often been commented on in the literature (e.g., Bergman, 1949; Cogger, 1979) and their structure has recently been studied (Gopalakrishnakone, 1985). The spines (or tubercles) are present in both sexes, although better developed in males, where they are usually present at birth. There is one spine per body scale. Extremely fragmented ventral scales may have one or (rarely) no spines, but in most ventrals two spines are present. Many males have well-developed spines on all the body scales, even on the tail, although the large head plates lack spines (some specimens have papillae on the head plates). Females are less spinose, although larger ones approach the spinosity of the males. Adult males and females may be readily sorted by visual inspection on the basis of spinosity.

Spines on scales are known in fishes as "nuptial tubercles" (Bond, 1979, p. 416) or "breeding tubercles" or "pearl organs" (Wiley & Collette, 1970, p. 147) and may serve at least three functions: "maintenance of body contact between the sexes during spawning; defense of nests and territories; stimulation of the females in breeding" (Wiley & Collette, 1970, p. 148).

Similar spines have been noted in many colubrids. "Knobbed anal keels" on the dorsal scales of the anal region have been observed in *Natrix* (= *Nerodia*), *Thamnophis*, *Diadophis*, *Carphophis*, and *Farancia* (Blanchard, 1931); in *Aspidura trachyprocta* (Davis, 1936, p. 273); in *Tropidoclonion lineatum* (Force, 1936); and in *Tretanorhinus* (Henderson & Hoevers, 1979). Low keels on dorsal scales have been recorded from adult male *Drymarchon corais couperi* (Layne & Steiner, 1984). Spines have also been observed on some sea snakes, e.g., *Hydrophis cyanocinctus* (Boettger, 1888) and *Thalassophina viperina* (Volsoe, 1939), and also occur on *Hydrophis ornatus* (Gritis, pers. obs.).

Generally these spines are considered to be non-seasonal in occurrence, although seasonality has been suggested for *Tretanorhinus nigroluteus lateralis* (Henderson & Hoevers, 1979), and for *Drymarchon* (Layne & Steiner, 1984). Although empirical data are lacking, we consider it likely that the spines in *Lapemis* play a role in courtship (stimulation) or copulation (enhancing body contact). It may be appropriate to note here that *Lapemis* is a distinctly shortbodied snake, the "short Hydrus" of Shaw (1802). Thus *Lapemis*, as opposed to some of the long slender *Hydrophis*, might be expected to possess adaptations to enhance contact during copulation.

The spines may influence locomotion by increasing both drag and turbulent flow. These factors, at least in fishes, seem to be more limiting in larger, fast swimming forms than they are in smaller, slow swimming forms (Alexander, 1974). Seahorses and trunkfish, for example, presumably swim well enough with spines (Hildebrand, 1974, p. 573). The sea snakes for which feeding behavior is known (including *Lapemis*) do not use fast swimming speeds to catch prey (Voris et al., 1978; Voris & Voris, 1983) and in absence of major predators flight speed may not be critical.

Acknowledgments

We thank the following institutions for the loan of specimens: The American Museum of Natural History (AMNH); The Academy of Natural Sciences, Philadelphia (ANSP); The California Academy of Sciences (CAS); The Carnegie Museum of Natural History (CMNH); The Los Angeles County Museum (LACM); The Museum of Comparative Zoology (MCZ); The Museum of Vertebrate Zoology, University of California (MVZ); The National Museum of Natural History, Smithsonian Institution (USNM); the Universitets Zoologiske Museum, Copenhagen (ZMUC).

We are grateful to Robert F. Inger, Hymen Marx, and Alan Resetar for helpful comments on this work. The figures were prepared by Zorica Dabich. Molly Ozaki and Jeanne Jendra graciously provided word processing expertise.

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- Sekinchang** — FMNH 198917; 198919–26; 198950; 198958–92; 198995; 198997–9001; 199004–05; 199051–52; Embryos: 198922(3); 198926(4).
- Singapore** — FMNH 213164–67; 213170; 213172; 213205–32; 213378–83; 213385–88; 213587–95; 215279–96; Embryos: 213216(5); 213228(2); 213382(2); 213383(3); 213587(2).
- Arabian Sea** — FMNH 207877–91; 208948–50; 210124; LACM 132104; ZMUC 66156.
- Philippines** — AMNH 2290; ANSP 6779; CAS 12432–36; CMNH 2352; 2354; 2359; 2365; 2368; 2370; 2373–74; 2377; 2381; 2385; 2388; 2390–96; FMNH 202827–30; 202932–33.
- Persian Gulf** — USNM 145795; ZMUC 66147–55; 66157.
- Burma** — FMNH 207892–95; 210126; 210131.
- S. India–Ceylon** — AMNH 76865; CAS 12305–07; 12431; FMNH 40752; 122529; 142451–52; 152501; MCZ 25980; 126380; USNM 166477; 167584–85; 195873–195873A; ZMUC 6656–59.
- Australia–New Guinea** — AMNH 87678–79; 111829–31; 115077–89; FMNH 97485; MCZ 149699–702; MVZ 77811.
- Thailand** — FMNH 152533; 178647; 178787–99; 178802–26; 178828–36; 178839–49; 178851–58; 178990–91; 178993–96; 179001–02; 191077; LACM 63539; 63564–68; 63570–92.
- North Borneo** — FMNH 63558; 130929; 131255–57; 133060–61; 133063–64; 133065; 133070; 133071; 133073–74; 133081–87; 141144–48; 141152–53; 141157–61; 142059; 142060–63; Embryos: 133065(5); 133070(5); 133073(4); 142059(4); 191890–94(5).

Appendix

SPECIMENS EXAMINED—**Sungei Buloh**—FMNH 197977–80; 197984–86; 198380; 198382–83; 198385–86; 198391–94; 198396–97; 198400–02; 198404–15;



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